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THE TAXONOMIC STATUS OF *CALOPTERYX XANTHOSTOMA* (CHARPENTIER, 1825) (ZYGOPTERA: *CALOPTERYGIDAE*)

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For the following reasons, *C.xanthostoma* (Charp.) should be considered a good species: (1) Its wing colour pattern is stable. All previously stated cases of intermediates with *splendens splendens* are *splendens* or *caprai*, not *xanthostoma*; (2) The coloured wing spot appears only a few days after emergence. In *splendens*, including the "intermediates", it is present from the beginning; (3) Where both species share the same area, there is a difference in habitat selection; (4) The colour of the ventral part of the ultimate abdominal segments is yellowish in *xanthostoma*, whitish in *splendens* (HEYMER, 1971b). This is an important character in reproductive isolation, probably as important as the wing spot itself; (5) The geographical area inhabitated lies greatly outside that of *C.splendens* and subspecies and is closed. It is the same area as the one occupied by a number of dragonflies, the specificity of which has never been challenged and that are very characteristic of it.

INTRODUCTION

The European and circum-mediterranean representatives of the genus *Calopteryx* differ from all other dragonfly groups in this area by building a cluster of very closely allied species. All attempts at finding good structural differences between them have so far failed and, despite so many efforts by a large number of investigators, it is generally felt that the present day situation is very unsatisfactory. The male anal appendages, the male copulatory organ, the female pronotum, the female ovipositor are all identical or virtually so in all species and subspecies. These features, which make up the classical tools for the study of dragonfly taxonomy, would lead to the conclusion that all representatives of *Calopterygidae* in the area under study belong to a single species.

Some additional characters of the wing venation, e.g. the structure of the postcostal field, appear to be more useful, but they have not been well studied in all taxa. Another feature which seems difficult to handle, and the value of which is unclear, is the size of the postocular tubercles (SCHMIDT, 1954).

Consequently, most recent keys (CONCI & NIELSEN, 1956; AGUESSE, 1968) turn to such characters as the wing shape, size and extent of the coloured wing spot in the male, sometimes in the female, colour of the ventrum of the terminal abdominal segments in the male. These characters being non-structural, have left many authors unsatisfied and uncertain. They have been applied merely *ad hoc* and not been well analyzed on their significance to the animals themselves. The decision whether they have specific or subspecific strength has always been an entirely arbitrary one. I therefore think we should tackle the entire problem anew, and the first question to be raised is by which means *Calopteryx*-species achieve reproductive isolation.

In most dragonflies, this is largely realized by structural differences between species. So to say, reproductive isolation is here synonym to morphological isolation. In itself, I consider this a rather strange phenomenon. Dragonflies are indeed eye-animals, and it is strange that visual stimuli are not made greater use of. Yet, I have recently stressed (DUMONT, 1972, in press) that in such genera as *Ischnura* and *Platycnemis*, only certain well-defined colour stages, before all in the female, are involved in copulation.

In *Calopteryx*, the combination of a good visual sense organ and bright wing and body colours results, as in many bird species, in a complex pre-copulatory behaviour (courtship display).

In this, the male is the agressive and active element, the female the receptive or passive element, that only delivers a positive or negative verdict to the male's approach.

This complex behaviour has been studied by BUCHHOLZ (1955), and has recently been taken up again and is being further developed by HEYMER (1970, 1971a, 1971b, 1972).

I shall not develop this reasoning much further here. The conclusion should, however, be that colour characteristics of the wing and the body, joint to a particular pattern of sexual behaviour, are undoubtedly equally valid in achieving reproductive isolation of species as any structural set of characters. If combined with a particular habitat selection, even within the same area as related "species", they may certainly be used as parameters for separating good species.

CALOPTERYX XANTHOSTOMA (CHARPENTIER, 1825): A GOOD SPECIES

The arguments presented above will now serve to prove that the *Agrion xanthostoma* described by TOUSSAINT DE CHARPENTIER in 1825 from the South of France, is a good species indeed. Selys, in SELYS & HAGEN (1850), refers to it as a subspecies of *C.splendens* (Harris, 1782), a treatment which has subsequently been accepted by most authors. It is, however, interesting to note SELYS' comments (1854:140): "J'aurais été très-disposé à regarder la *xanthostoma* comme une espèce distincte, si je n'avais eu sous les yeux des exemplaires qui tiennent le milieu entre les deux races". The two "races" referred to are the present *Calopteryx splendens splendens* and *C.xanthostoma*. The intermediate specimens, that were later termed "sous-variété intermédiaire" (SELYS & HAGEN, 1854) have been subsequently split off as a separate subspecies by CAPRA (1945), sub *C.splendens intermedia*, a preoccupied name, and again by CONCI & NIELSEN (1956), sub *C. splendens caprai*. The latter is a doubtful taxon, owing to the lack of stability of the male wing spot, the main character upon which it was based. KIAUTA (1971) has shown that the chromosome morphology tends to be as variable as the insect itself. LACROIX (1915, 1919) who published a series of papers on the fauna of South-West France, has also commented upon the *xanthostoma* problem. In one contribution (1919:100), he states: "dans la région de l'Ouest on trouve tous les intermédiaires entre la race *septentrionale* bien définie et *xanthostoma* et j'ai pu, dans ma collection, faire une série très intéressante". This statement refers to samples collected on the Boutonne river, Dépt. Charente. It was on the same river, in the same locality (St. Julien de l'Estephe, near St. Jean d'Angély) that the same author took its enigmatic *C. splendens faivrei*, photographs of which were published by us earlier (DUMONT, 1971). I visited the Boutonne River, while prospecting in South-West France, June 1969. Here, there exists a population of *C.splendens* with very variable wing spots, ranging from typical *C.splendens splendens* to a form coming close to *C.xanthostoma*. However, among several hundreds of specimens taken, not a single one had the wing apex entirely covered by blue colours. There is always a narrow hyaline border left (Fig. 1). But I found *xanthostoma* populations on the much larger river Charente, at Angoulème, and still on the Rivers Dordogne and Lot. Very dense populations of *C. xanthostoma* were found on the Célé River, an affluent of the Lot, while some *C. splendens caprai* occurred on the River Vers, another much smaller affluent of the Lot flowing in the valley next to that of the Célé.

From all the data gathered, one important statement could be derived: all populations of *C.xanthostoma* seen were completely homogeneous. All males had wing spots reaching invariably to the wing apex. All *C.splendens caprai* populations were very variable, but no true *xanthostoma* were seen among them.

It so appears that the variability character which stopped Selys from conserving Charpentier's species at the full species rank, is only at work in so-called *caprai* populations, but that the reverse is not true, i.e. *xanthostoma* is always typical.

It goes without saying that, in order to establish such a fact, one has to go and watch living populations. If only a museum collection is available, the conclusion

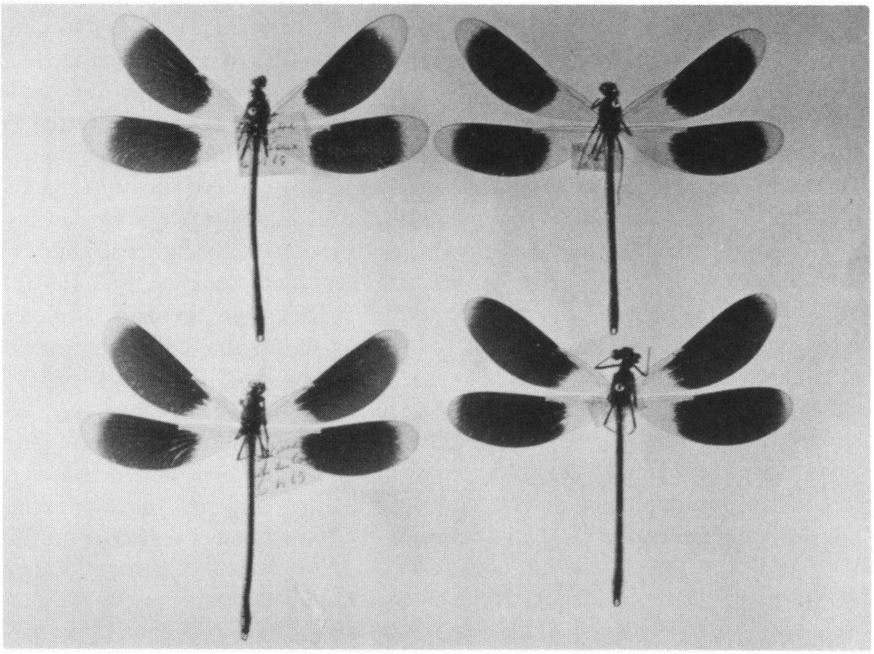

Fig. 1. Some males of *C.splendens* (Harris) from the Boutonne River, France, June 26, 1969., illustrating the variability of the coloured wing band in that population.

to be drawn from it would inevitably be the one arrived at by Selys, or recently, by LOHMANN (1970). Lacroix should have observed the real facts of nature, but

drawn from it would inevitably be the one arrived at by Selys, or recently, by LOHMANN (1970). Lacroix should have observed the real facts of nature, but

he failed to do so, probably influenced herein by Selys's writings.

It is not possible to defend the argument that the intermediate specimens are hybrids. For in that case more than half the male population on the Boutonne and probably elsewhere as well would be hybrids, but without genuine *xanthostoma* present to have produced them. Also, if these hybrids were sterile or with a decreased fecundity, these populations would decrease exponentially to zero, and there are no facts that support this point. Since Lacroix's time, the Boutonne population has not changed. Finally, I have seen these supposed hybrids copulate at the same rate and in the same way as the "normal" males.

A second argument in favour of *xanthostoma*'s specificity is in the post-emergence maturation phase in the males. This again has already struck Selys, and it certainly contributed in making him hesitate over the nature of the animal in question.

Quoting from Selys, in SELYS & HAGEN (1850:140): "les mâles très jeunes ont les ailes complètement transparentes ..... la race septentrionale même n'offre jamais cette complète absence de bande enfumée". This remark is pertinent, and was repeated in SELYS & HAGEN (1854). Figure 2 presents a series of *xanthostoma* males from the river Célé, on which this gradual development of the blue wing band as a function of age can clearly be identified. I may add that freshly emerged specimens from the intermediate populations ("*caprai*") all have the wing spots well indicated from the beginning. This time lag in colour development between *xanthostoma* and *splendens* is clearly a genetically determined difference between the two groups.

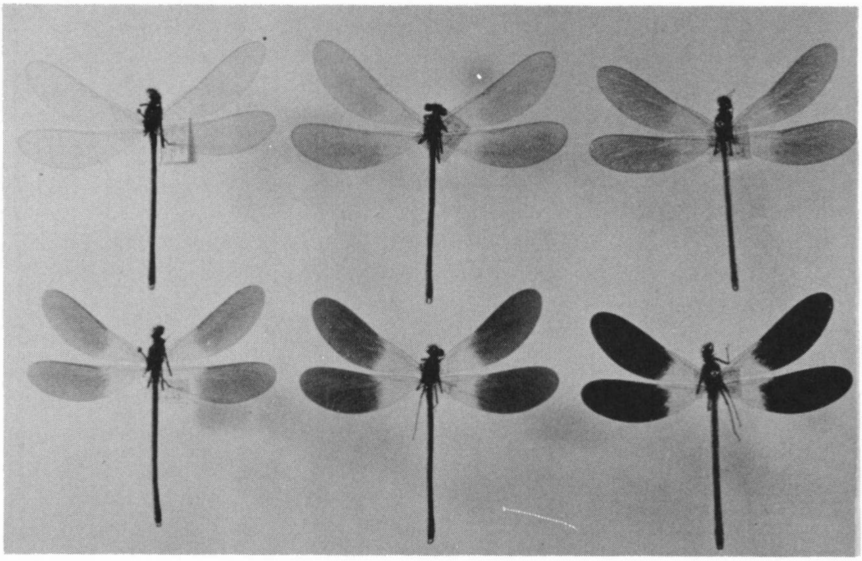

Fig. 2. Some males of *C.xanthostoma* (Charp.) from the Célé River, France, June 24, 1969, showing the gradual development of the coloured wing band. The youngest specimen (upper left, wings completely hyaline) is two days old.

A third argument, already briefly mentioned before, is the different habitat selection between *splendens* and *xanthostoma*. Although they share the same geographic area in e.g. South-West France, I have never seen them cohabit. In South-West France, *xanthostoma* selects larger rivers, and *splendens-caprai* smaller ones. But in the South of Spain, where *xanthostoma* is, as far as known, the only member of the *splendens* group present, I have also seen it on smaller rivulets (e.g. in the Cordoba area, July 1971), where it may co-occur with *C.haemorrhoidalis*. This habitat displacement in different areas is to be seen as a mechanism to avoid interspecies competition.

A fourth character has been stressed by HEYMER (1971b). The ventrum of the ultimate segments of the male abdomen, very important during courtship display, are yellowish in *xanthostoma*, whitish in *splendens splendens* and *splendens caprai*. These colours are not well preserved on dried specimens, turning to brownish tinges. In living animals, this character and the wing colour pattern are the main criteria by which a female may identify a male as conspecific. It may well be stressed that visually, one readily identifies a flying *xanthostoma* from a *splendens*-male, however narrow the hyaline wing border in the latter may be.

A few additional differences between *xanthostoma* and its congeners, that have been known for a long time, are also more or less valid, e.g. the relative narrowness of the wings in both sexes, and the ultimate abdomen segments in the female that are less shiny than in *splendens*. The latter character is, however, frequently subjective.

In general, it is much more difficult to identify *Calopteryx* females than males. This again is a consequence of the reproductive behaviour, in which the female takes few or no initiatives.

A fifth and final argument, in my opinion, is to be found in the geographical distribution of the species. It inhabits South-West and South France, Liguria (Italy), the surroundings of Lugano in Switzerland (LIEFTINCK, pers. comm.) and the whole of Spain. SELYS (1850) claims to have received specimens from Algeria, Sicily and Sardinia. Later, he even added Corsica (SELYS, 1854). If it may not be excluded that the range of *xanthostoma* extends to North-Africa, it should be stressed that it has been never found in Morocco and that recent data from Algeria are lacking.

Likewise, its occurrence in Sicily, Sardinia and Corsica has never been confirmed. The southern limit of *xanthostoma*'s occurrence in Italy is uncertain. If it extends as far as Campania or even further south, it must be rare there anyway. The area occupied is a closed one, and agrees to a fair extent with that of this very particular fauna inhabiting South-West and South France and Spain. It embraces such forms as *Calopteryx virgo* (?) *meridionalis*, *Platycnemis acutipennis*, *Platycnemis latipes*, *Gomphus graslini* and *Macromia splendens*. The least that can be said is that this curious analogy can hardly be a coincidence. It goes without saying that I cannot accept to synonymize the *Calopteryx xanthostoma*-like *Calopterygidae* that live in the eastern basin of the Mediterranean with the West-mediterranean animals.

If the coloured wing spot is important in reproductive isolation, it should be clearly realized that the limits between which it can vary are either complete absence or complete covering of the wing, with all in-between possibilities. Both extremes have indeed been realized in nature, the former even twice. Further, intermediate possibilities have also, in certain cases, evolved more than once, in different geographical locations. The lack of migration and the great selective value of the character certainly favour such convergences largely.

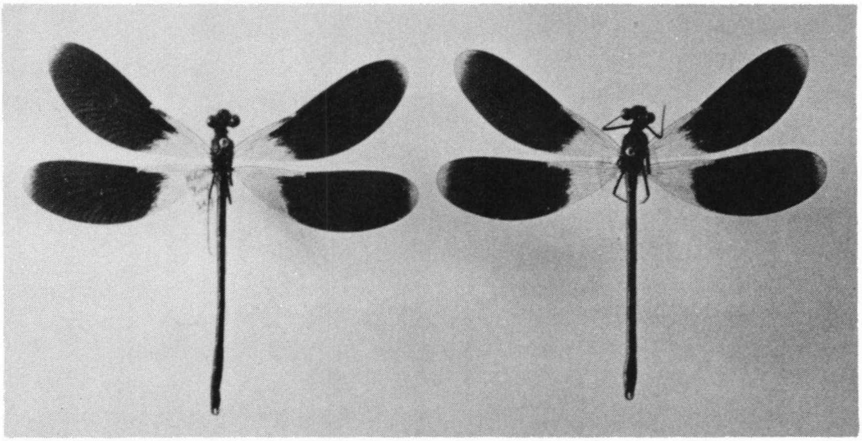

Fig. 3. Male of *Calopteryx splendens balcanica* Fudakowski (left); male of *Calopteryx splendens caprai* (?) Conci & Nielsen (right). For comments, cf. text.

Figure 3 shows two *Calopteryx* males: left, an extreme male of *C.splendens balcanica* (wing top well hyaline; usually it is more extensively or entirely covered by blue-black); right, an extreme male of *C.splendens caprai* (wing top extensively covered with blue-black, usually hyaline border wider). The only difference between the two animals is the slightly superior size of the former. I can hardly imagine that, on such evidence, one would synonymize both taxa. Clearly, in *Calopteryx* the working unit is not the individual, but the population!

The variability of *C.xanthostoma* wings is limited to the two same wing types recognized by ST. QUENTIN (1932) in *C.splendens*: the short and smoothly rounded spot type (Fig. 4a) and the long and irregularly bordered type (Fig. 4b). Each type is more or less confined to isolated populations. A mixed form is rare.

Finally, SELYS (1887) states to have received an aberrant homochromic female from the Charente area (France). The specimen, still in existence, is shown in Figure 5. It is not another *faivrei*-like animal, as I had first expected it to be, but it bears close relationship to some of the oriental *Calopterygidae*. I am unable to place this animal correctly, but, I feel, an error in the indication of its origin may have been made by Delamain, who presented the animal to Selys. There has indeed never been reported a second specimen of similar nature from the same area and there are no other cases of homochromic females in *C.xanthostoma* on record.

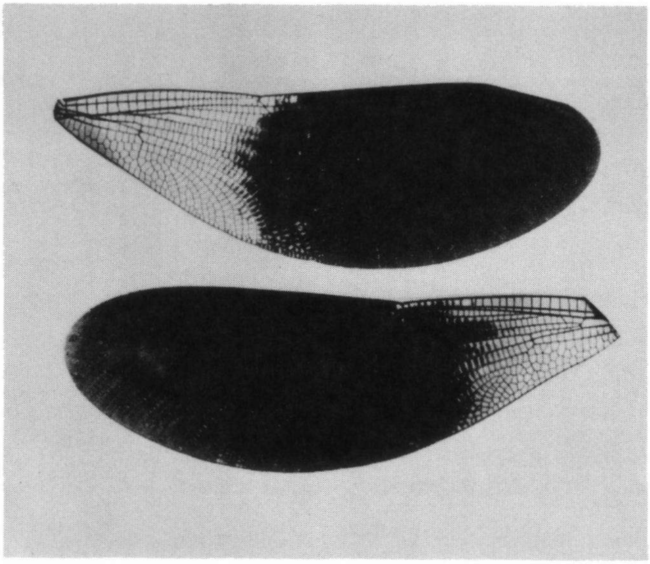

Fig. 4. The two forms of wing spots in *C.xanthostoma*. Upper one: smoothly rounded, smaller spot (Gard, France, July 1959). Lower one: large, irregularly randed spot (Dordogne, Les Eyzies, France, June 1969).

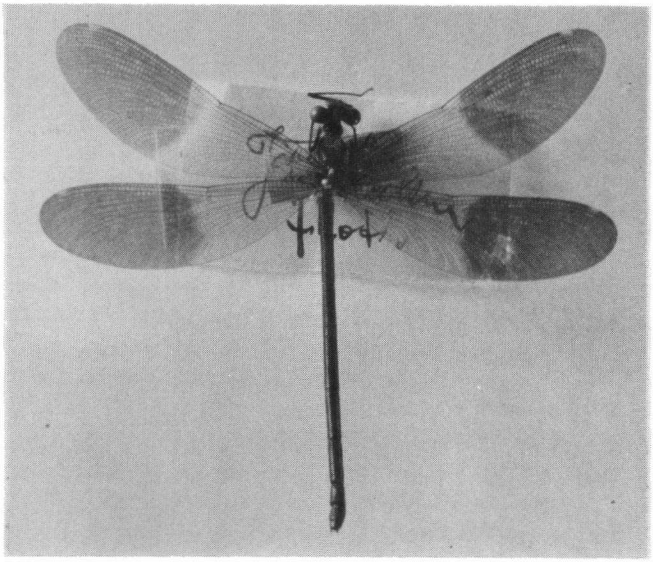

Fig. 5. The homochromic *C.xanthostoma* (?) female from the Charente, France, presented to Sélys by Delamain.

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